concentrating proteins in secretory granules. What did the stack, the most prominent component of the Golgi apparatus, contribute? Marian Neutra and Charles Leblond (1969, p. 103) posed the question:

> Why do these proteins pass through the Golgi apparatus? Do they undergo some essential processing operation there? One can see with the electron microscope that proteins come out of the apparatus neatly packaged in globules whose membranes have been donated by the Golgi saccules. It seems hardly likely, however, that this elaborate system exists simply for the purpose of putting the proteins in bags; nature has a way of avoiding complex solutions for simple problems. We therefore decided that a closer look had to be taken at the protein products themselves to determine if their sojourn in the Golgi apparatus was responsible for some important change in their chemical form.

An important clue was that most secretory products are not proteins alone, but rather proteins linked to carbohydrates. Leblond and his collaborators at McGill University studied the goblet cell of the colon, which secretes such a compound – mucigen. These goblet cells are long, narrow structures squeezed between other cells in the intestinal lining. Each contains several Golgi stacks of eight to ten saccules. The bottom or *cis* saccules are flattened in appearance, whereas the top or *trans* saccules are bulging with material. Above them are mucus globules that are excreted in due course. In autoradiographic studies with Marian Peterson, Leblond showed that glucose tracer first appeared in the cisternae of the Golgi apparatus five to fifteen minutes after injection and moved progressively to the more distal cisternae, with the distal cisterna being converted into mucigen granules (Peterson & Leblond, 1964a; Peterson & Leblond, 1964b). Subsequently, Neutra and Leblond (1966a; 1966b) proposed that the glucose or galactose precursors enter the goblet cell from a capillary and move directly to the Golgi apparatus, where glucose is combined with proteins synthesized in the endoplasmic reticulum to form glycoproteins. As Neutra and Leblond (1969) related, by the end of the 1960s evidence had accumulated that the Golgi apparatus performed a variety of roles in the construction of large carbohydrate molecules such as adding sulphate bonds to create polysaccharide secretion products.

After decades during which it was suspected to be an artifact, in the 1960s the Golgi apparatus came to be generally recognized as a major component of the machinery of the cell. In part its rehabilitation stemmed from the ability of the electron microscope to provide more detailed images of its structure, but of even greater significance was the development of an account of its functional significance in the generation of products that figured in cell secretions processes.